

Does a Polyphagous Predator Prefer Prey Species That Confer Reproductive Advantage?: Case Study of *Podisus maculiventris*

JESUSA CRISOSTOMO LEGASPI AND BENJAMIN C. LEGASPI, JR.¹

USDA-ARS-CMAVE/CESTA-Center for Biological Control, 310 S. Perry-Paige Building,
Florida A&M University, Tallahassee, FL 32307

Environ. Entomol. 33(5): 1401–1409 (2004)

ABSTRACT The purpose of this study was to determine whether preferred prey of *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae) adult females also conferred maximal fecundity. We also studied egg development and maturation as a function of predator age, i.e., “ovigeny” as used predominantly in the context of parasitoids. To determine prey preference, adult females were simultaneously offered five pest prey: 1) beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae); 2) fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae); 3) cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae); 4) greater wax moth, *Galleria mellonella* (L.) (Lepidoptera: Pyralidae); and 5) yellow mealworm, *Tenebrio molitor* (L.) (Coleoptera: Tenebrionidae) ($n = 20$). In a second experiment, adult *P. maculiventris* females were provided a single species of prey (for each of the five prey species, $n = 10$). This experiment was repeated over four durations: 7, 15, 22, and 30 d. After each time trial, egg load dissections were performed, and numbers of mature and immature eggs were recorded. *P. maculiventris* displayed a preference of beet armyworm, whether measured as numbers attacked or estimated biomass consumed. However, no significant differences were found in cumulative numbers of eggs laid under the different prey treatments, with the exception of the 22-d trial where significantly more eggs were laid when feeding on the cabbage looper. During the 22-d trial, the number of egg clutches and numbers of eggs per clutch were highest when fed cabbage looper and lowest with yellow mealworm. Percentage of egg hatch combined across time trials was highest in cabbage looper (81.7%) and lowest in greater wax moth (63.8%). Egg load dissections revealed that the total number of eggs and numbers of mature eggs declined significantly with predator age. However, numbers of immature eggs increased. The mean number of mature eggs in 7-d-old predators represented only $\approx 5\%$ of mean cumulative numbers of eggs laid by 30-d-old predators, indicating that *P. maculiventris* is strongly synovigenic, where egg development and maturation continues during adulthood. The implications of these results are discussed from the context of *P. maculiventris* as a biological control agent.

KEY WORDS prey preference, predator fitness, ovigeny

WHEN PRESENTED SIMULTANEOUSLY with a choice of several prey species, a polyphagous predator might be expected to select prey that would be of the best nutritional quality and allow maximal fecundity. It is conceivable that preference for nutritious prey would convey reproductive advantages that would be favored by natural selection, thereby propagating this trait in subsequent generations. However, empirical evidence shows that qualities other than nutritional value affect predator selection of prey. In choice experiments, the bigeyed bug *Geocoris punctipes* (Say)

(Heteroptera: Geocoridae) attacked more frequently and consistently pea aphid, *Acyrtosiphum pisum* (Harris) (Homoptera: Aphididae), in preference to eggs of corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), despite the greater nutritional value of the eggs to *G. punctipes* (Eubanks and Denno 2000). *G. punctipes* survived 4 times as long on and completed development only on the *H. zea* eggs than on aphids. In *G. punctipes*, prey choice was determined not by nutritional value but by preference for mobile prey. Strohmeyer et al. (1998) studied the effect of prey species consumed by the spined soldier bug, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), on several biological parameters on three species of Lepidoptera: *Manduca sexta* (L.) (Sphingidae), *Junonia coenia* Hübner (Nymphalidae), and *Vanessa cardui* (L.) (Nymphalidae). *P. maculiventris* ate more caterpillars of *M. sexta* and *J. coenia* than *V. cardui*.

This article presents the result of research only. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the United States Department of Agriculture or the Agricultural Research Service of any product or service to the exclusion of others that may be suitable.

¹ Employed by State of Florida, contact through senior author.

Final dry weight was higher in treatments fed *M. sexta* or *V. cardui* than *J. coenia*. However, relative growth rate was fastest on *V. cardui*, which was consequently deemed the best prey species for *P. maculiventris*.

The study of insect "ovigeny" (egg production and development during adulthood) was developed for parasitoids because of the direct effect of egg load on parasitism rates, and hence reproduction. We are not aware of published studies where the concept of ovigeny has been applied to predators. However, ovigeny has been studied in Lepidoptera (Boggs 1997) and is a "potentially unifying concept for aiding understanding of the evolution of life-history strategies among insects generally" (Jervis et al. 2001). Parasitoid species where adults emerge with a fixed complement of mature eggs are termed "pro-ovigenic," whereas species that display continued egg development during adulthood are termed "synovigenic" (Heimpel and Rosenheim 1998, Carbone and Rivera 2003). A synovigenic parasitoid may experience short-term egg depletion, although lifetime fecundity limitation should be rare (Carbone and Rivera 2003). Egg limitation has been demonstrated in the field, impacting host-parasitoid population dynamics, possibly including inverse density-dependent parasitism rates (Heimpel and Rosenheim 1998). In this study, we presented *P. maculiventris* with several choices of prey species to determine whether prey selected preferentially also resulted in highest fecundity. We also investigated ovigeny in this predator through time series dissections performed in the laboratory.

Materials and Methods

Prey Preference. A laboratory colony of *P. maculiventris* was maintained at USDA-ARS-CMAVE/CESTA-Center for Biological Control at Florida A&M University, Tallahassee, FL, in a Thermo Forma model 3740 growth chamber (Thermo Forma, Marietta, OH) at 26°C and a photoperiod of 14:10 (L:D) h. Adult female *P. maculiventris* [2–3-d old, fed *Tenebrio molitor* (L.) (Coleoptera: Tenebrionidae)] were starved for 24 h and individually placed in the middle of a plastic petri dish (15 cm in diameter) lined with filter paper that served as the feeding arena. The following species of prey were provided to the predator: beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae); fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae); cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae); greater wax moth, *Galleria mellonella* (L.) (Lepidoptera: Pyralidae); and yellow mealworm, *T. molitor*. Three larval prey (third-fourth instar) of each species were kept in screened plastic petri dishes (3.5 cm in diameter). Each dish with the prey species was placed in a circular pattern inside the feeding arena. This allowed feeding by the predator but prevented prey species from mixing with each other. The predator was placed in the center of the arena and allowed to feed for 24 h, after which the number of prey attacked was recorded. The experiments were performed inside the growth chambers. The weights

of prey individuals selected at random was also recorded ($n = 10$). Estimates of biomass consumed were obtained by multiplying numbers of prey consumed with mean prey weight for that species. Predator consumption was measured both in terms of numbers of prey eaten and estimated biomass consumed. Live body weights were obtained using a Mettler PB 3002 analytical balance (Mettler Toledo, Hightstown, NJ) with a precision of ± 0.0001 g, and weights were converted from grams to milligrams. Temperature and relative humidity inside the chamber were monitored by HOBO recorders (Onset Computer Corp., Bourne, MA). The experiment was replicated 20 times.

Effect of Prey on Fecundity. Female *P. maculiventris* adults used in this experiment were collected from a laboratory colony described above. Two- to 3-d-old *P. maculiventris* were individually placed in a plastic petri dish (15 cm in diameter) lined with filter paper. The same prey species mentioned above were provided to the predator. One larval prey (third-fourth instar) was provided daily to the predator. A damp cotton ball on a plastic petri dish (3.5 cm) was kept in the feeding arena to provide moisture to *P. maculiventris*. Each female was then provided a mating opportunity with a male from the laboratory colony every 3 d after the start of the experiment. Eggs laid by each female predator were counted and removed daily. For each prey species treatment except females sacrificed at 30 d after the start of the experiment, we recorded preoviposition period, number of eggs per clutch, size of first egg clutch, and number of egg clutches laid. Average age at first oviposition or the day the first clutch was laid was calculated only for females that oviposited. A series of experiments were conducted whereby predators were sacrificed at 7, 15, 22, and 30 d after the start of the experiment to measure egg loads at different ages of *P. maculiventris*. Eggs from females that were sacrificed at 22 d after the start of the experiment were held for eclosion. Egg masses were kept until they hatched in the growth chamber in the same conditions as described above, to calculate percentage of hatch of egg masses from the latter females. The experiment was replicated 10 times.

Egg Load Dissections. After females were sacrificed at the assigned ages, they were kept in a Revco model ULT 1786-3-A36 (Kendro Laboratory Products, Asheville, NC) ultra-low freezer at -80°C for egg load dissections. Variable numbers of females under the different assigned ages were dissected because females did not live to the age that was assigned. The dorsal and ventral abdominal body walls of the females were separated, and the number of eggs in the ovaries was counted. Eggs were classified as mature (bigger, dark-colored, rough texture, and chorion prominent) and immature (smaller, light-colored, smooth texture, and chorion not prominent).

Statistical Analysis. Numbers of prey consumed and estimated prey biomass consumed were analyzed by one-way analysis of variance (ANOVA) by using Systat 10 software (Systat Software, Inc., Richmond, CA). For each feeding time trial, prey diet was tested for effects on cumulative numbers of eggs. One-way

ANOVA was performed on the effects of prey diet on numbers of egg clutches, numbers of eggs per clutch, numbers of eggs in the first clutch, and day the first eggs were laid within each time trial. Percentage of egg hatch was analyzed across trials after performing an angular transformation. However, means are presented as untransformed percentages (Sokal and Rohlf 1995). Where treatment effects were significant, means were separated using Tukey honestly significant difference (HSD) test at $P = 0.05$. Egg load analyses were performed using a General Linear Model (SYSTAT 2002) where numbers of eggs was the dependent variable; predator age and prey species consumed were independent. Analyses were separated into total egg load (immature + mature eggs), numbers of immature eggs, and numbers of mature eggs. Separate linear regressions were performed for numbers of immature, mature, and total eggs as a function of predator age.

Results

Prey Preference. Significant differences were found in the mean number of prey eaten by *P. maculiventris* provided different prey species. Results indicated that *P. maculiventris* preferred beet armyworm ($F = 8.6$; $df = 4, 95$; $R^2 = 0.27$; $P < 0.01$). Consumption means of the other prey species were not significantly different (Fig. 1A). Mean weights of the prey were as follows: beet armyworm, 174.5 ± 11.4 (mean milligrams \pm SE); fall armyworm, 230.4 ± 19.8 ; cabbage looper, 179.4 ± 9.9 ; greater wax moth, 362.9 ± 23.9 ; and yellow mealworm, 142.9 ± 4.8 . Analysis of estimated biomass consumed was similar to that of numbers of prey consumed (Fig. 1B). *P. maculiventris* consumed significantly higher biomass of beet armyworm compared with the other prey offered ($F = 5.9$; $df = 4, 95$; $R^2 = 0.2$; $P < 0.01$).

Effect of Prey on Fecundity. In all experiments, the age of first oviposition of *P. maculiventris* ranged from 4 to 7 d. In the 7-d feeding trial, no significant differences were found in the cumulative number of eggs laid per female under the different prey treatments ($F = 1.3$; $df = 4, 43$; $R^2 = 0.11$; $P = 0.30$) (Fig. 2A). The 15-d feeding trial also produced no significant differences ($F = 1.8$; $df = 4, 33$; $R^2 = 0.18$; $P = 0.16$) (Fig. 2B). In the 22-d trial, *P. maculiventris* laid significantly more eggs per female when feeding on the cabbage looper, than on the wax moth or mealworm, with other feeding treatments intermediate ($F = 7.3$; $df = 4, 28$; $R^2 = 0.51$; $P < 0.01$) (Fig. 2C). Treatment effects were again insignificant in the 30-d trial ($F = 1.3$; $df = 4, 13$; $R^2 = 0.3$; $P = 0.31$) (Fig. 2D).

The effects of prey diet on number of egg clutches, mean number of eggs per clutch, number of eggs in the first clutch, and the day first clutches were laid are summarized in Table 1. The only significant effects found within time trials were again in the 22-d trial, where numbers of egg clutches and eggs per clutch were highest in cabbage looper (17.5 and 18.18, respectively) and lowest in yellow mealworm (10.5 and 9.6, respectively). Pooled percentage of egg hatch was

highest in cabbage looper (81.7%) and lowest in greater wax moth (63.8%). As in cumulative fecundity, data on egg clutches suggest that cabbage looper is a marginally superior diet for *P. maculiventris*.

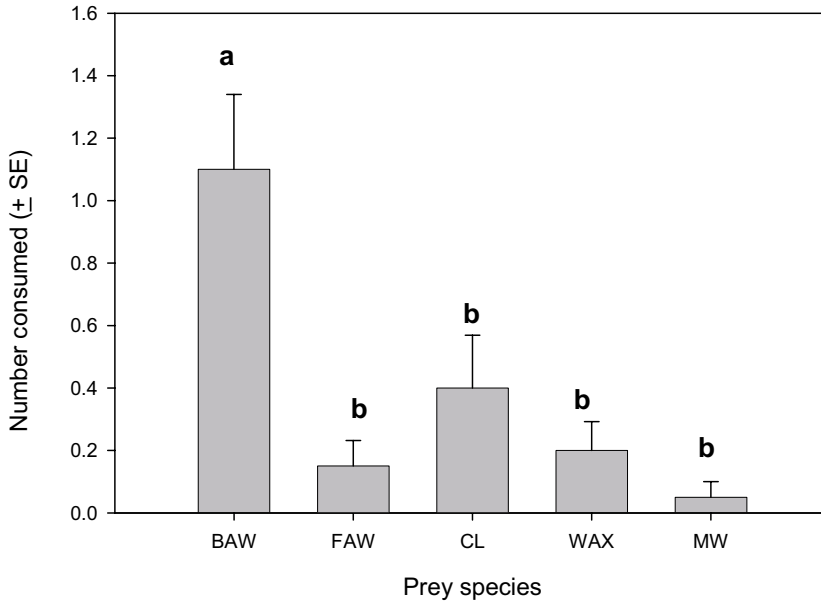
Egg Load Dissections. Analysis using the General Linear Model showed that total egg load was significantly affected by predator age ($F = 13.7$; $df = 1, 127$; $R^2 = 0.15$; $P < 0.01$), but not by prey species consumed ($F = 1.9$; $df = 4, 127$; $R^2 = 0.15$; $P = 0.11$). Because prey species consumed did not significantly affect egg loads, data were pooled in regression analyses for the effects of predator age on numbers of immature, mature, and total eggs. Total number of eggs declined significantly as a function of predator age and was described by the equation $Eggs_{total} = 20.98 - 0.397 \text{ age}$ (SE constant = 1.84; SE slope = 0.1) ($F = 14.4$; $df = 1, 131$; $R^2 = 0.1$; $P < 0.01$) (Fig. 3A). However, numbers of immature eggs increased with age: $Eggs_{immature} = 1.15 + 0.44 \text{ age}$ (SE constant = 1.09; SE slope = 0.09) ($F = 50.2$; $df = 1, 131$; $R^2 = 0.28$; $P < 0.01$) (Fig. 3B). Numbers of mature eggs was again described by a declining function: $Eggs_{mature} = 19.83 - 0.83 \text{ age}$ (SE constant = 1.51; SE slope = 0.09) ($F = 95.2$; $df = 1, 131$; $R^2 = 0.42$; $P < 0.01$) (Fig. 3C).

The mean number of mature eggs in 7-d-old *P. maculiventris* was 16.5 ± 1.6 (\pm SE, $n = 67$). Cumulative number of eggs laid by 30 d was 328.6 ± 39.2 ($n = 5$), suggesting that only 5% of mature eggs were present early in the predator's life. Using this estimate, *P. maculiventris* is strongly synovigenic.

Discussion

P. maculiventris is a polyphagous predator known to feed on >75 insect species (McPherson 1980, McPherson et al. 1982), several of which are important pests (Waddill and Shepard 1975, Lopez et al. 1976). Prey species chosen for this study are important insect pests and documented prey of *P. maculiventris*. Prey preference was measured using both numbers of prey consumed and estimated biomass of the prey eaten. Both methods tend to overestimate prey consumption because not all prey items were fully consumed. Furthermore, the experimental design is assumed to have no influence over preferences for prey items. Both measures resulted in the same general conclusion: *P. maculiventris* preferred beet armyworm to the other prey offered. Analysis of cumulative fecundity under the different feeding times and prey treatments was more ambiguous. Results did not show a strong preference for nutritionally valuable prey for female reproduction. Within each time trial, only the 22-d trial yielded statistically significant results: cumulative fecundity was highest on cabbage looper prey and lowest on greater wax moth and yellow mealworm. In the 7- and 15-d trials, it is possible that feeding time was insufficient to allow treatment effects to become measurable. Loss of significant treatment effects in the 30-d trial may be attributed to the fewer number of replicates that survived to 30 d, thereby resulting in higher variability. Except for the 7-d trial, the data suggest that feeding on cabbage looper resulted in

A: Number of Prey Consumed



B: Estimated Prey Biomass Consumed

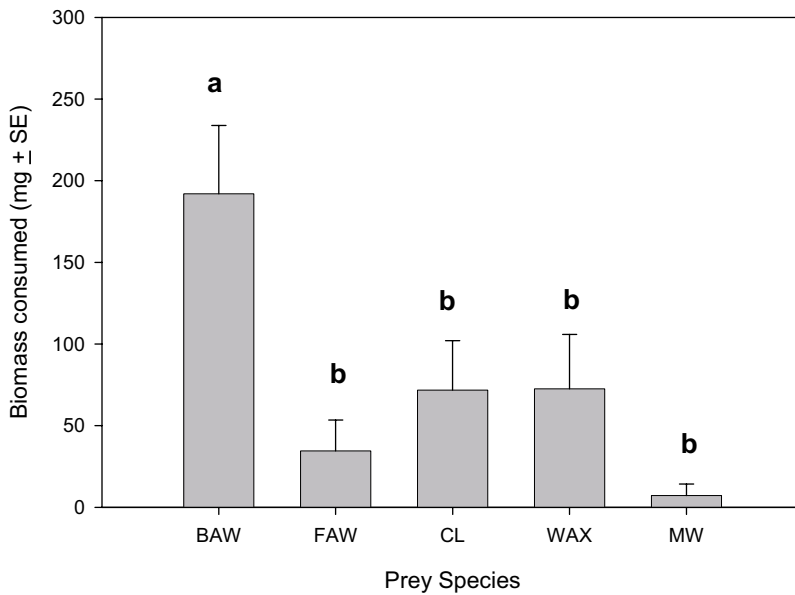


Fig. 1. (A) Mean number of prey attacked by *P. maculiventris* provided different prey species. Highest numbers attacked were beet armyworm ($F = 8.6$; $df = 4, 95$; $R^2 = 0.27$; $P < 0.01$). Other prey species were not significantly different (Tukey HSD, $P = 0.05$). (B) Analysis of estimated biomass consumed yielded similar results to that of numbers attacked ($F = 5.9$; $df = 4, 95$; $R^2 = 0.2$; $P < 0.01$).

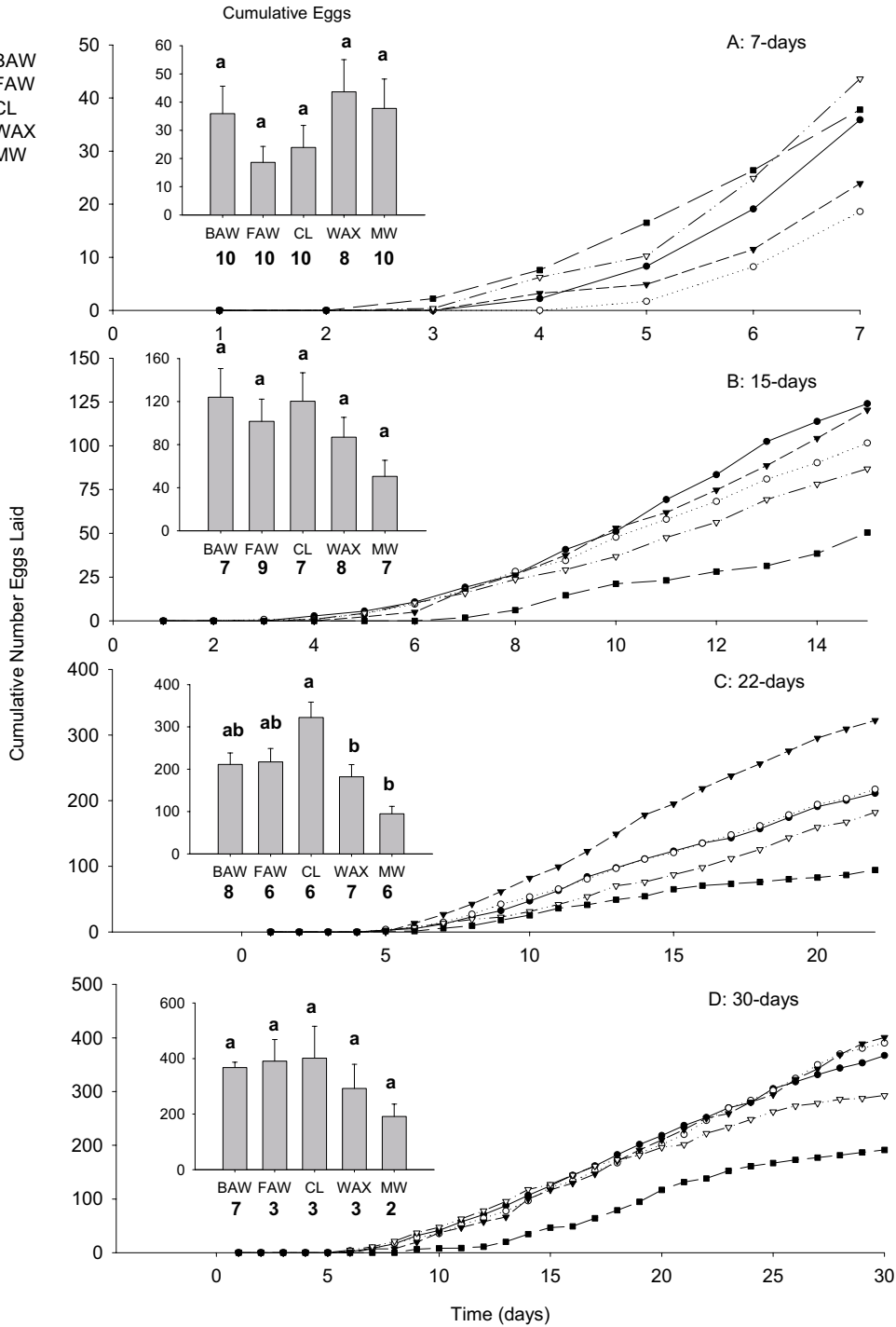


Fig. 2. Effect of prey preference on cumulative fecundity for (A) 7-d trial, (B) 15-d trial, (C) 22-d trial, and (D) 30-d trial. Prey species were BAW, beet armyworm; FAW, fall armyworm; CL, cabbage looper; WAX, greater wax moth; and MW, yellow mealworm. Only the 22-d trial produced significant treatment effects where *P. maculiventris* laid significantly more eggs per female when feeding on the cabbage looper than on the wax moth or mealworm, with other feeding treatments intermediate ($F = 7.3$; $df = 4, 28$; $R^2 = 0.51$; $P < 0.01$) (C).

Table 1. Effects of prey diet on oviposition of *P. maculiventris*

Time trial	Prey species ^a			Statistics ^b		
	BAW	FAW	CL	WAX	MW	F
7-day trial						
No. egg clutches	1.89 ± 0.39	0.90 ± 0.23	1.10 ± 0.28	2.13 ± 0.58	2.20 ± 0.55	2.32
Eggs/clutch	16.04 ± 3.6	13.90 ± 3.4	15.92 ± 3.34	18.06 ± 3.39	12.78 ± 2.88	0.38
Eggs in 1st clutch	11.56 ± 3.27	12.40 ± 3.07	15.90 ± 3.41	16.75 ± 4.11	10.00 ± 2.40	0.80
Day 1st clutch laid	4.00 ± 0.78	4.30 ± 0.96	4.90 ± 0.86	4.88 ± 0.85	3.80 ± 0.85	0.34
15-day trial						
No. egg clutches	8.57 ± 1.90a	7.44 ± 0.87a	7.71 ± 0.87a	7.38 ± 0.84a	4.00 ± 0.72a	2.39
Eggs/clutch	12.59 ± 2.26a	12.83 ± 1.85a	14.44 ± 1.96a	10.73 ± 1.50a	12.20 ± 1.42a	0.52
Eggs in 1st clutch	13.86 ± 3.36a	9.11 ± 1.47a	13.57 ± 2.99a	8.25 ± 1.85a	13.14 ± 1.96a	1.36
Day 1st clutch laid	5.71 ± 1.25a	6.67 ± 0.65a	7.57 ± 0.81a	7.13 ± 0.90a	9.43 ± 1.00a	2.11
22-day trial						
No. egg clutches	14.50 ± 1.39ab	13.83 ± 1.68ab	17.50 ± 1.06a	13.14 ± 1.18ab	10.50 ± 1.91b	2.73
Eggs/clutch	14.44 ± 1.14ab	15.51 ± 1.58ab	18.18 ± 1.15a	13.43 ± 1.40ab	9.60 ± 1.87b	4.44
Eggs in 1st clutch	10.38 ± 1.72	16.00 ± 3.65	12.50 ± 2.58	6.29 ± 1.61	7.83 ± 2.40	2.49
Day 1st clutch laid	6.50 ± 0.46	8.17 ± 1.47	6.00 ± 0.26	6.86 ± 0.67	7.83 ± 1.11	1.06
30-day trial						
No. egg clutches	21.86 ± 1.28	18.33 ± 3.93	13.00 ± 1.73	18.67 ± 4.67a	14.50 ± 5.50	1.26
Eggs/clutch	18.07 ± 2.39	22.15 ± 4.65	30.05 ± 5.13	15.26 ± 0.87	14.06 ± 2.26	2.87
Eggs in 1st clutch	12.29 ± 2.74	15.33 ± 7.97	13.67 ± 3.48	10.33 ± 3.67a	8.00 ± 5.00	0.28
Day 1st clutch laid	7.73 ± 0.48	7.67 ± 0.88	8.67 ± 1.67	10.00 ± 2.31	9.00 ± 1.00	0.83
Egg Hatch ^c	72.9 ± 3.0%ab (n = 131)	72.8 ± 3.2%ab (n = 112)	81.7 ± 2.5%a (n = 121)	63.8 ± 3.9%b (n = 102)	77.8 ± 3.2%ab (n = 62)	3.8

^a BAW = beet army worm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae); FAW = fall army worm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae); CL = cabbage looper, *Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae); WAX = greater wax moth, *Galleria mellonella* (L.) (Lepidoptera: Pyralid); MW = yellow mealworm, *Tenebrio molitor* (L.).

^b One-way ANOVA of oviposition measurement, as affected by prey species; where F-statistic is significant, means are separated by Tukey HSD; means followed by different letters are significantly different ($P = 0.05$).

^c Data from all time trials combined; angular transformation performed on percentage data before one-way ANOVA; means are presented as untransformed percentages.

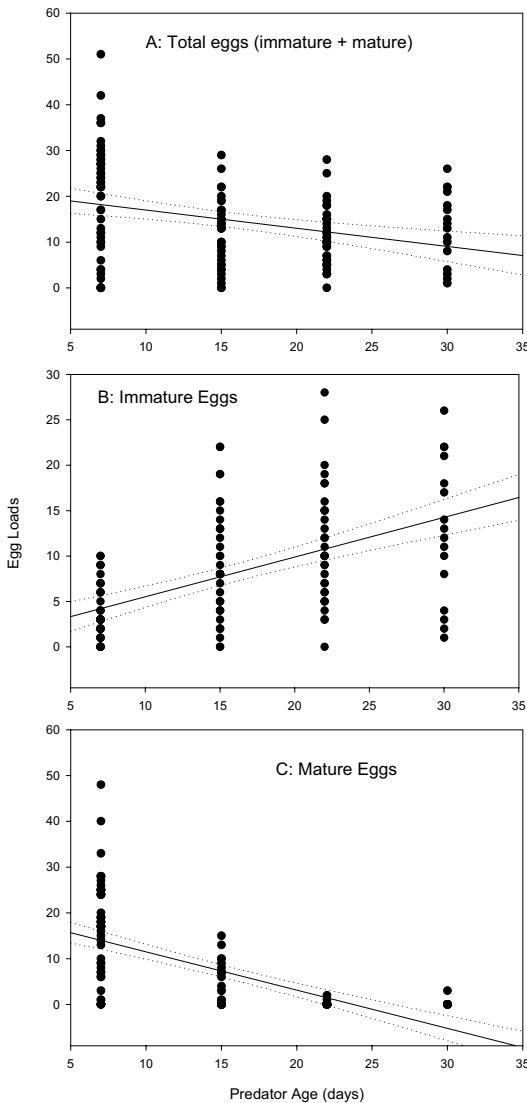


Fig. 3. Egg load dissections. Regressions shown are for (A) total number of eggs with age, (B) numbers of immature eggs with age, and (C) numbers of mature eggs with age. Regression equations are (A) $Eggs_{total} = 20.98 - 0.397 \text{ age}$ ($F = 14.4$; $df = 1, 131$; $R^2 = 0.1$; $P < 0.01$), (B) $Eggs_{immature} = 1.15 + 0.44 \text{ age}$ ($F = 50.2$; $df = 1, 131$; $R^2 = 0.28$; $P < 0.01$), and (C) $Eggs_{mature} = 19.83 - 0.83 \text{ age}$ ($F = 95.2$; $df = 1, 131$; $R^2 = 0.42$; $P < 0.01$), respectively.

highest cumulative fecundity, whereas feeding on yellow mealworm resulted in the lowest. Data on egg clutches also suggested that feeding on *T. ni* can produce higher numbers of egg clutches, eggs per clutch, and percentage of egg hatch.

When we compared the results of the prey preference experiment with those of the cumulative fecundity, we found that in both cases, the yellow mealworm diet produced consistent results. *P. maculiventris* preferred other prey types over yellow mealworm, and the yellow mealworm diet resulted in

poor fecundity for the predator. However, feeding on its preferred prey, the beet armyworm, resulted in only intermediate levels of cumulative fecundity for *P. maculiventris*. The highest reproductive output was recorded in the 22-d trial when feeding on cabbage looper, a prey species that was consumed at less than half the rate of the beet armyworm. Therefore, we found no evidence to support the hypothesis that *P. maculiventris* will preferentially consume prey types that will result in highest predator fecundity and that factors other than reproduction may have been used to select prey.

Using predatory spiders as a model, Toft (1999) argues that active prey selection seeks an optimal compromise among three nutritional goals: 1) maximize energy intake; 2) balance nutritional intake; and 3) minimize toxic consumption, by recognition of associated prey tastes and behavior. In many predation studies, polyphagous predators are presented with a single species of prey. When more than one choice is presented simultaneously, the predator can improve its fitness or fecundity by feeding on mixed diets, or by choosing larger prey items. For example, *Podisus nigripinus* (Dallas) displayed higher egg and nymphal production on a diet of *T. molitor* and *Musca domestica* L. (Diptera: Muscidae) offered simultaneously or on alternate days, compared with diets consisting of either species exclusively (Zanuncio et al. 2001). In addition, nymphs of *P. maculiventris* were found to develop faster when fed pupae rather than larvae of *T. molitor*, or caterpillars of *G. mellonella* (de Clercq et al. 1998). Nymphal survival and adult weights of the predator were the same on all three diets. However, females reared on *G. mellonella* produced about twice as many eggs (≈ 1000 per female) than on larvae or pupae of *T. molitor*.

A preference for nutritious prey can therefore convey reproductive advantage to the predator. For the trait to persist by natural selection, it must be inheritable. Saint-Cyr and Cloutier (1996) analyzed parental factors determining prey selection in the generalist predator *Perillus bioculatus* (F.), which is most often recorded as a predator of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). Additionally, unusual prey offered were the yellow mealworm and house cricket, *Acheta domestica* (L.). Nymphs reared from parents fed yellow mealworm still fed more frequently on the beetle than cricket, suggesting genetically inherited preference for *L. decemlineata*. Saint-Cyr and Cloutier (1996) suggested genetically inheritable and maternally reinforcing specialization of *P. bioculatus* on the Colorado potato beetle or related prey. Therefore, polyphagous predators may increase reproductive fitness by selecting nutritious prey species. Furthermore, this reproductive advantage may be inheritable and therefore favored by natural selection. Under this scenario, we might expect polyphagous predators to display preference for the most nutritious prey species. Empirical evidence shows this is not always the case (Strohmeyer et al. 1998). *G. punctipes* displayed preference for the pea aphid in preference to the more nutritious eggs of the

corn earworm (Eubanks and Denno 2000) because prey choice was determined not by nutritional value but by preference for mobile prey. Excluding prey in the form of sessile eggs, this strategy might be sound because mobile prey are often the best quality.

Prey selection may be determined by factors other than prey nutritional value in relation to maximizing reproduction. A predator may display preference toward prey species that are less able to escape or defend themselves against predator attack (van Emden 1995). In laboratory prey preference experiments, *P. maculiventris* was more successful in feeding on fifth instars of *Spodoptera littoralis* (Boisduval) than on fourth instars of southern green stink bug, *Nezara viridula* (L.) (de Clercq et al. 2002). After a 24-h feeding period, 72.5% of *S. littoralis* were killed versus only 5% of *N. viridula* because stinkbug immatures displayed greater agility and success in escaping *P. maculiventris*. In predatory spiders [*Pardosa* (Lycosidae) and *Habronattus* (Salticidae)], gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), larvae escaped predation, possibly due to protection afforded by its long setae (Bardwell and Averill 1996).

In reviewing the literature on ovigeny in parasitoids, Jarvis et al. (2001) rejected the concept of a fixed dichotomy, and defined an "ovigeny index" as the proportion of maximum potential lifetime complement that is mature at female emergence. The index ranges from 0 (extreme synovigeny) to 1 (extreme pro-ovigeny). More than 98% of parasitoid species surveyed by Jarvis et al. (2001) emerged with at least some immature eggs. These authors also argue that synovigenic species tend to be longer lived, and suggest a biological cost in early reproductive effort in pro-ovigenic species. However, Bennett et al. (2002) caution that this finding may be an experimental artifact. This study suggests that *P. maculiventris* is a strongly synovigenic predator because only $\approx 5\%$ of mature eggs are present in 7-d-old predators, relative to cumulative oviposition of 30-d-old predators. Furthermore, the number of immature eggs increased with age, indicating continual egg production during adulthood. The decline in total egg load with age indicates that egg production did not keep pace with oviposition, and numbers of mature eggs declined with predator age.

In conclusion, we found no evidence that *P. maculiventris* preferred prey species that conferred maximal fecundity. However, limitations imposed by the experimental design (screened petri dish arena) prevented prey from exhibiting factors such as defense, hiding, or escape that is often critical in nature. The use of a more field-realistic experimental design may yield different results. Adult females seem to be strongly synovigenic, which probably has minimal effect on its efficacy as a biological control agent, compared with factors such as reproductive rate. All other factors being equal, we might prefer a control agent that selected prey that maximized its reproduction. In terms of egg production, synovigeny may not be as beneficial to a predator as it is to a parasitoid because its reproduction, as well as suppression of the host, is

not as strongly linked to its ability to lay eggs. However, as in parasitoids, synovigeny may confer an ability to increase reproduction during periods of favorable environment or prey availability, leading to greater density-dependent host regulation.

Acknowledgments

We thank Drs. Muhammad Hasseb and Wills Flowers (Florida A&M University) and two anonymous reviewers for valuable comments on earlier versions of this manuscript. Mohamed Soumare (Florida A&M University) helped rear *P. maculiventris* colony in the laboratory. William Allen, Jeffery Head, and Elizabeth Aninakwa (Florida A&M University undergraduate students) also assisted in this study. We acknowledge Nancy Lowman and Dr. Robert Meagher, Jr. (USDA-ARS-CMAVE) for rearing and providing the insect prey species.

References Cited

- Bardwell, C. J., and A. L. Averill. 1996. Effectiveness of larval defenses against spider predation in cranberry ecosystems. *Environ. Entomol.* 25: 1083–1091.
- Bennett, D. M., K. T. Reynolds, L. J. Thompson, and A. A. Hoffmann. 2002. Individual trade-offs and artifacts in the egg parasitoid *Trichogramma carverae* (Hymenoptera: Trichogrammatidae). *Ann. Entomol. Soc. Am.* 95: 695–700.
- Boggs, C. L. 1997. Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* 78: 181–191.
- Carbone, S. S., and A. C. Rivera. 2003. Egg load and adaptive superparasitism in *Anaphes nitens*, an egg parasitoid of the eucalyptus snout-beetle *Gonipteris scutellatus*. *Entomol. Exp. Appl.* 106: 127–134.
- de Clercq, P., F. Merlevede, and L. Tirry. 1998. Unnatural prey and artificial diets for rearing *Podisus maculiventris* (Heteroptera: Pentatomidae). *Biol. Control* 12: 137–142.
- de Clercq, P., K. Wyckhuys, H. N. de Oliveira, and J. Klapwijk. 2002. Predation by *Podisus maculiventris* on different life stages of *Nezara viridula*. *Fla. Entomol.* 85: 197–202.
- Emden, H. F. 1995. Host plant-Aphidophaga interactions. In J. P. Aeschlimann, D. Horn, M. Mackauer, and P. Wellings [eds.], Paper presented at the 5th International Symposium of the International Organization for Biological Control Global Working Group on Ecology of Special issue: augmentation and enhancement of Aphidophaga. *Agric. Ecosyst. Environ.* 52: 3–11.
- Eubanks, M. D., and R. F. Denno. 2000. Health food versus fast food: the effects of prey quality and mobility on prey selection by a generalist predator and indirect interactions among prey species. *Ecol. Entomol.* 25: 140–146.
- Heimpel, G. E., and J. A. Rosenheim. 1998. Egg limitation in parasitoids: a review of the evidence and a case study. *Biol. Control* 11: 160–168.
- Jervis, M. A., G. E. Heimpel, P. N. Ferns, J. A. Harvey, and N.A.C. Kidd. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny.' *J. Anim. Ecol.* 70: 442–458.
- Lopez, J. D., R. L. Ridgway, and R. E. Pinnel. 1976. Comparative efficacy of four insect predators of the bollworm and tobacco budworm. *Environ. Entomol.* 5: 1160–1164.
- McPherson, J. E. 1980. A list of the prey species of *Podisus maculiventris* (Hemiptera: Pentatomidae). *Great Lakes Entomol.* 13: 18–24.

- McPherson, R. M., J. C. Smith, and W. A. Allen. 1982. Incidence of arthropod predators in different soybean cropping systems. *Environ. Entomol.* 11: 685–689.
- Saint-Cyr, J. F., and C. Cloutier. 1996. Prey preference by the stinkbug *Perillus bioculatus*, a predator of the Colorado potato beetle. *Biol. Control* 7: 251–258.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman & Co., New York.
- Strohmeyer, H. H., N. E. Stamp, C. M. Jarzomski, and D. Bowers. 1998. Prey species and prey diet affect growth of invertebrate predators. *Ecol. Entomol.* 23: 68–79.
- SYSTAT. 2002. SYSTAT Software, Inc., Richmond, CA.
- Toft, S. 1999. Prey choice and spider fitness. *J. Arachnol.* 27: 301–307.
- Waddill, V., and B. M. Shepard. 1975. A comparison of predation by the predators *Podisus maculiventris* and *Stretus achoraga* of the Mexican bean beetle *Epilachna varivestis*. *Ann. Entomol. Soc. Am.* 68: 1023–1027.
- Zanuncio, J. C., A. J. Molina-Rugama, J. E. Serrao, and D. Pratissoli. 2001. Nymphal development and reproduction of *Podisus nigrispinus* (Heteroptera: Pentatomidae) fed with combinations of *Tenebrio molitor* (Coleoptera: Tenebrionidae) pupae and *Musca domestica* (Diptera: Muscidae) larvae. *Biocontrol Sci. Tech.* 11: 331–337.

Received 3 November 2003; accepted 9 June 2004.
